Book review: The evolution of beauty

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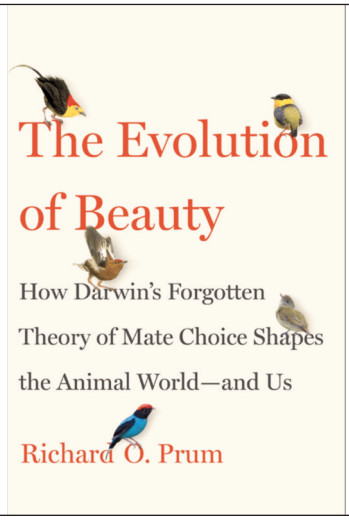
Prum R.O. 2017. The evolution of beauty. How Darwin's forgotten theory of mate choice shapes the animal world – and us. Doubleday, New York. 428 pp. ISBN 978-0-385-53721-6. €26.



Having explained, in the opening pages, the feelings of a serious birder when getting to know a new bird species, "connecting familiarity and personal experience to facts and understanding", Richard Prum goes on to argue that "we need an evolutionary theory that encompasses the subjective experiences of animals in order to develop an accurate scientific account of the natural world. We ignore them at our intellectual peril, because the subjective experiences of animals have critical and decisive consequences for their evolution". At this point it became clear to me that I was reading the work of an argumentative intellectual innovator, perhaps an intellectual dare-devil? Throughout reading his book, Prum gave me flushes of excitement by his recognition of capacities (in birds) and processes (in evolution) that certainly were not part of my university curriculum, but seem to make so much sense. "By recognizing sexual signals as beautiful to those organisms that prefer them – whether they are Wood Thrushes, bowerbirds, butterflies, or humans – we are forced to engage with the full implications of what it means to be a sentient animal making social and sexual choices."

So what is 'The Evolution of Beauty' about? It is about the puzzle of explaining the evolution of the huge diversity of sizes, shapes, sounds, plumages and 'extended' parts of the phenotype (bowerbird bowers, woven weaver nests, etc.) among the 10,000 species of birds (see Prum *et al.* 2015 for the most recent reconstruction of the evolutionary bush of birds since the demise of the dinosaurs at the end of the Cretaceous). It examines Darwin's second big idea about organismic evolution (Darwin 1871). In addition to 'natural selection' (the selective weeding of functionally poorer variants), he proposed an unrelated evolutionary force called 'sexual selection'. In Darwin's original formulation, sexual selection refers to the aesthetic choices for mates made by prospecting partners. Based on the perception and subjective evaluations by other individuals, in the mating game particular phenotypes gain an advantage over others because they are considered beautiful. Many such individual mating decisions then cumulatively shape the evolution of the phenotype.

In sexual selection, organisms act as the agents of their own evolution! Sexual selection implies three more things. (1) It gives the key role to the choosiest sex. (2) The pursuit of subjective experiences can lead to maladaptive mate choices (which will then be held in check by the other evolutionary force, 'adaptive' natural selection). And, (3) as the task of attracting a mate is so much more unconstrained and open-ended than the task of being a good forager and survivor in a particular environment, sexual selection will lead to phenotypes that are quirky, historically contingent, individualized and unpredictable (given a certain environmental context). "The result is the earth's nearly unfathomable variety of biological beauty."

The ideas that females are in the lead and that sexual selection can result in functionally maladaptive phenotypes did not sit well with Darwin's contemporaries. It still does not, and the past generation of evolutionary biologists has worked hard to subsume sexual selection as a category *within* adaptive natural selection. In this version, beauty is desirable because it signals true adaptive benefits such as health, vigour and good genes: beauty is an 'honest advertisement'. This is what so many ornithologists are trying to show today, probably with mixed success, and probably generating a literature biased towards confirmatory studies. It is ironic how all this work ignored a century of theoretical underpinning of Darwin's original version of sexual selection (Prum 2010, 2012).

Prum proposes that, instead of seeking confirmation for the adaptive features of mate choice, as is the case in contemporary evolutionary biology, studies of mate choice should always consider a null model to explain phenotypic extravagance. This null model, the

'Beauty Happens' hypothesis of the book, predicts the evolution of 'arbitrary traits that are neither honest or dishonest, indicate nothing other than mating availability, and lack any meaning or design other than their potential to correspond to mating preferences' (Prum 2010). This would provide a theoretical framework in which we would have to design tests to reject the null hypothesis, thus open-mindedly collecting support for adaptive explanations – currently the only accepted framework – , and work towards an unbiased scientific literature on the evolution of ornaments.

It was interesting to read, in a book on the origin of art (Rothenberg 2011), about the history and wider implications of Prum's ideas. It turns out that a tropical ear infection halfway through his career, put an end to Prum's reliance on hearing as his main observational tool and bird sound as his scientific focus of interest. Instead, he shifted gear to the visual world and started working on bird shapes, making fundamental discoveries on the evolutionary origin of feather design, including their colour patterning. This is very personal, and in the book he develops another theme which will be personal to almost all potential readers: mate choice and the evolution of human sexual dimorphic sizes, shapes and behaviours. For a 'feminist ornithology', and a gripping account on what it is like to be a female (and, indeed, a male) in monkey and ape societies, consult the chapters occupying the latter half of the book.

Of course, I tried to see how the Beauty Happens hypothesis could help me understand phenomena in my own field, the long-distance migration of shorebirds (Piersma *et al.* 2001). This includes the extreme variation in breeding plumages of males of one such long-distance migrant, the enigmatic Ruff *Philomachus pugnax*. Do the plumage variations of one behavioural phenotype, the resident male Ruffs (van Rhijn *et al.* 2014), 'simply' represent the arbitrariness of sexual selection sensu Darwin and Prum? The tension, or rather the eventual balance, between natural and sexual selection may actually show up in the design of cranes (Gruidae). Apparently, accepting that beauty happens, Jones & Witt (2014) suggest that longer migrations have led to the adaptive evolution of smaller body size, but that the force of sexual selection has selected for the particular beauty of their auditory signals. The outcome of these opposing selection forces has given the smaller crane species, i.e. those making the longest migrations, an elongation of their sound producing organ, the trachea.

'The Evolution of Beauty' was a thoroughly good and stimulating read. Sure, Prum delivers some strong advocacy here, which easily comes at a cost of bias, but I didn't mind so much considering what is at stake. It encouraged my growing conviction that biology should be ready to reinvent itself, and that this requires seriously looking afresh at the natural world from several different angles. I loved spending time with the book, and started missing it as soon as I was finished.

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